The Flora of Australia as a Measure of the Antiquity of the Angiosperms

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INTRODUCTION

IF ONE INTENDS to consider as difficult a problem as the early history of a large land area, Australia would seem to be particularly suitable for such a study: its long geographic isolation and the great number of scientific investigations to which it has been subjected make it a natural choice.

Australia's land connection with the island groups of Malaysia (except for New Guinea) was ended in the Upper Cretaceous period. According to physicists' calculations, based on the rates of disintegration of radioactive elements, about 30–40 million years have passed since the Eocene epoch in early Cenozoic time. Inasmuch as the Upper Cretaceous period occurred before the Eocene epoch, it can be concluded that, on the whole, the Australian flora and fauna have remained undisturbed for an extremely long time. Under these circumstances of isolation, ancient forms of plant and animal life have been preserved, while, during the long periods since the isolation began, new species of plants and animals have developed from them as well. It must not be forgotten, however, that immigration also has occurred, introducing new species into Australia's plant and animal life since the beginning of its geographic isolation.

The many investigations into the animal life of Australia have given unequivocal evidence of the continent's isolation. Today the most primitive mammals—the Monotremata (Ornithodelphia) and the species of Echidna, Proechidna, and Ornithorhynchus—appear only in Australia and in New Guinea. These mammals resemble reptiles more than any of the other mammals because they lay eggs, have a cloaca, and still possess the number of shoulder bones of primitive animals. As fossil evidence has shown, their ancestors appeared during the Triassic formation, to become, in fact, the first of the mammals. They increased in number during the Jurassic period, but, to a great extent, they died out as early as the Eocene epoch. In Australia, however, some of these primitive mammals have survived to this day, affording us illustration of the concept of "endemism by conservation."

The marsupials, too, are notably typical of Australia. They are not limited to Australia, for there are opossums in North and South America, and Chironectides in South America; but the great majority of the marsupials is found only in Australia. They have developed there, it is interesting to observe, in a manner analogous to the development of placental mammals of the other continents, notably the carnivores, rodents, insectivores, and ungulates.

The survival of the Monotremata and of the Marsupialia can be attributed to the fact that, before man's appearance on the Australian continent, no other placental mammals existed in Australia to prey upon them. There were only mice, which sometimes wandered on driftwood from island to island, and bats; but these were not significant enemies. (It may be possible, of course, that the mice and the bats first arrived in Australia in times subsequent to the Upper Cretaceous period and, therefore, subsequent to the be-

ginning of Australia's geographic isolation.) As far as the dingo is concerned, it is supposed that aboriginal Austral inhabitants entering Australia from Malaysia were the first to bring this animal to the southern continent.

It is also pertinent to our thesis to note that zoologists believe that some of the opossums (Caenolestes) migrated to North America from South America. Fossils of Marsupialia have been found in Europe and in North and South America, an indication that they must have been distributed over vast regions of the earth. The Marsupialia have survived chiefly in Australia, and for this reason Australia today has the oldest and most primitive mammal types in the world.

Now because, geologically speaking, mammals and angiosperms are of about the same age, it is natural to ask if the oldest and most primitive of the flowering plants are also to be found in Australia today. The answer to this question would help us to determine the antiquity of the angiosperms.

This is a question that is difficult to answer, if only because botanists are not in agreement on the most primitive species of angiosperms. This one question asks other questions: If the earliest species of angiosperms could be defined, would it be found that they exist preeminently or even exclusively in Australia? Or, if the earliest species cannot be defined, is it possible to determine, from the Australian flora of today, which are the most primitive species of angiosperms that have succeeded in persisting until this time? These are the problems to be investigated in this paper.

WHAT ARE THE MOST PRIMITIVE FAMILIES OF THE FLOWERING PLANTS?

As every botanist knows, the question of primitiveness in flowering plants is a controversial one. Some think that certain species of the Monochlamydeae are the most primi-tive, while others think that the Polycarpicae among the Choripetales are the most ancient. Once, even certain of the Monocotyledones (the Pandanales) were considered for the distinction, although this claim, of course, could not be proved by any significant arguments. Inasmuch as this is hardly the place for a discussion of the phylogenetic criteria by which plants are judged, the more pertinent portions of my book, *Neue Ziele der Botanik* (1938), are suggested for reference.

If, in our search for the oldest angiosperms, and in our analysis of the Australian flora, we hold the opinion that those families which are put at the head of the Monochlamydeae in the Engler and Prantl system of classification are the ones which show the most primitive characteristics, we should be supported in this assumption by the Casuarinaceae found in Australia. In their original distribution they extended from Sumatra to the Philippines, New Caledonia, and the Fiji archipelago (Diels, 1926), and to Tahiti, the Austral Islands, and the Marquesas (Brown, 1935). As yet, however, there is no reliable basis for the hypothesis that the Casuarinaceae are more nearly related to the Gymnospermae than is any other family of the Angiospermae. Neither can this supposition be proved for the Proteaceae and the Balanopsidaceae, which are also placed at the beginning of the Monochlamydeae in the Engler and Prantl taxonomic system. In Australia more than half of all of the species of Monochlamydeae are Proteaceae (about 600 species), although the family has extended to southern Africa, southern Asia, and South America (Vester, 1940). The species of Proteaceae are almost exclusively ligneous plants, which would indicate that, phylogenetically, they are rather an old group, but in the absence of paleontological evidence we cannot be certain that these species are really older than many others we might consider, so we have to be content only with supposing that they *might* be.

On the other hand, if we hold the opinion, as many botanists do, that the Polycarpicae are the most primitive of the Angiospermae, we should find that only two very small families of Polycarpicae are endemic in Australia: the Eupomatiaceae and the Himantandraceae, which are related to the Eupomatiaceae, but which possess neither calyx nor corolla (Diels, 1919: 126 *et seq.*). The other families of Polycarpicae are not well represented in Australia: the Magnoliaceae afford only 4 species, the Annonaceae 18, the Nymphaeaceae 5, the Ranunculaceae 17, and the Myristicaceae 1. In view of these facts, it cannot be claimed that the Polycarpicae are the most primitive of angiosperms in Australia and that a comparison with the preservation of the earliest mammals could be made.

This brief appraisal is enough to show that the angiosperms which most botanists consider to be the oldest of flowering plants (Polycarpicae) do not exist exclusively or preeminently in Australia. But in the information we have learned about the Casuarinaceae and the Proteaceae we may have found certain clues which will be of value later when we investigate their degree of primitiveness.

WHICH SPECIES OF ANGIOSPERMS
PERSISTING IN AUSTRALIA ARE
THE MOST PRIMITIVE?

Now we can set about answering the second question, inquiring into the conclusions which can be drawn from a study of the history of the Australian flora. At first it may seem questionable in itself to compare the early histories of flowering plants with those of mammals, particularly when it is realized that the conditions governing their migrations were quite different. We assume that those mammals living in Australia during the Upper Cretaceous period have been isolated since that time because of the continent's isolation, and that only rarely have they been joined by later immigrants. Can the same assumption be made for the flower-

ing plants? Or may those various plant species now found in Australia have migrated to the continent since its separation because they—or rather, their seeds—could cross the ocean gap while the animals were not able to do so?

To obtain a general view of the whole flora of Australia, let us consider the catalogue of F. von Mueller, his *Census of Australian Plants* (1889). Because of the recent advances in our knowledge, Mueller's list is neither complete nor infallible, yet it is not likely that the proportions of the numbers of species within large groups and of the endemic species have changed significantly since that time. Therefore we may use the *Census* without hesitation, all the more necessarily because there does not exist a later catalogue for the whole Australian territory (including Tasmania but not New Zealand).

Mueller's catalogue lists 8,842 species, and, because it does not mention those species introduced in recent times (since about 1800), it is well fitted for our purpose. Of these 8,842 species, 7,734 (that is, 87.5 per cent) are endemic in the larger sense of the word—that is to say, they are found in Australia itself but may also extend to New Zealand and to parts of Polynesia as well. The percentage of endemism is extremely high.

Table 1 may serve for comparison of the percentage of endemic plants found in Australia with those found in other parts of the world.

As a matter of fact, it is probable that among the 8,842 species listed in Mueller's *Census of Australian Plants* there may be a great many species which were introduced by man, although this hypothesis cannot be substantiated in its details. If this is true, however, the percentage of endenism in Australia would be even higher than it is here calculated.

There is no doubt but that the longer a country has been isolated the more endemics

TABLE 1

REPRESENTATION OF ENDEMIC PLANTS IN
AUSTRALIA AND IN OTHER PARTS
OF THE WORLD

REGION	APPROXIMATE PERCENTAGE OF ENDEMIC PLANTS	REFERENCE
Australia	87.5	calculated from Mueller, 1889.
New Zealand	73	calculated from Cheeseman, 1925.
Hawaii	90	according to St. John, 1946.
Galapagos	40	calculated from Stewart, 1911.
Sokotra	33	according to Drude, 1896.
Balkans	26	calculated from Hayek and Markgraf, 1927–1933, and from Turrill, 1929.
Iceland	0	calculated from Ostenfeld and Gröntved, 1934.

For statements about smaller islands, see O. Drude, *loc. cit.*

it shows; and we may assume that, other conditions being equal, the percentage of its endemism would enable us to measure the length of its period of isolation. Scandinavia, for example, has very few endemics (and these are "weak" endemics in the systematic sense) because there was not enough time for it to be overgrown with flowering plants be-

fore the sparse soil-cover left by the retreating glaciers was removed by erosion, and because the short period during which alluvial soil has been collecting since glaciation has not been long enough for the development of many new species. It is true, of course, that Scandinavia can hardly be compared with Australia, inasmuch as the prevailing temperatures in Scandinavia are not at all favorable for the formation of new species (Sterner, 1943: 84).

Even if we considered as not being endemic to Australia those plants which are also found in New Zealand and in Polynesia, there remain, nevertheless, 7,501 species, or 84.8 per cent, which are limited to continental Australia and Tasmania. Obviously the reduction in number is a minor one.

An appreciation of the manner of the distribution of endemic species among the larger plant groups of the Australian flora will be gained from Table 2, which shows that among the Angiospermae, at least, the endemic species are quite equally distributed among the three groups into which the angiosperms are divided, with 89.3 per cent for the Sympetalae, 90.2 per cent for the Dialypetalae, and 92.9 per cent for the Monochlamydeae. This high number of endemics is not shared by the Monocotyledones, among which only 79.7 per cent of the species are

TABLE 2

DISTRIBUTION OF ENDEMIC SPECIES AMONG THE LARGER PLANT GROUPS
OF THE AUSTRALIAN FLORA

PLANT GROUP	TOTAL NUMBER OF SPECIES IN GROUP	PERCENTAGE OF WHOLE FLORA REPRESENTED BY GROUP	NUMBER OF ENDEMIC SPECIES IN GROUP	PERCENTAGE OF TOTAL NUMBER OF ENDEMIC SPECIES IN GROUP
Pteridophytae	244	2.7	124	50.8
Gymnospermae	43	0.5	43	100.0
Monochlamydeae	1,130	12.8	1,050	92.9
Dialypetalae	3,641	41.2	3,286	90.2
Sympetalae	2,229	25.2	1,991	89.3
Monocotyledones	1,555	19.6	1,240	79.7
Totals	8,842	100.0	7,734	87.5 of the total number

endemic. Relatively speaking, they show the smallest number of endemics among the angiosperms, which is rather an interesting fact, inasmuch as in the flora of European countries a certain parallel can be found for these values (Schmidt, 1945).

The smaller percentage of endemics among the Pteridophytae may be explained by the fact that the ferns are more readily disseminated over greater distances by means of their spores. It may be that in this manner many species of ferns immigrated into Australia, or emigrated from it, after its geographical isolation had begun. The same supposition is valid for many species of the Gramineae and for the Cyperaceae among the Monocotyledones.

When we consider the great number of endemics present in the Australian flora, we are tempted to jump to the important conclusion that, in later times, only an inconsiderable migration of plants took place into Australia from abroad. If there had been any considerable degree of migration, we should be able to find the species of plants now living in Australia spread over other continents as well, and especially over Malaysia. Actually, however, they are not so widely distributed, but are confined as endemics to Australia. The evidence is such that we may safely conclude, therefore, that a pronounced development of species took place on the Australian continent *after* the geographical isolation had begun. But, if few species have migrated into Australia from abroad over such a very long time (except in the cases of the Pteridophytae, which show the fewest endemics), is it not probable that all of the types which evolved into endemic species were already in existence *before* the period of geographical isolation, that is, during the Upper Cretaceous period? Did the numerous representatives of the characteristic families of the Australian flora already flourish in those ancient times? Was the Australian flora of those days similar, at least in its families,

to the Australian flora as it is now? Above all, did all of the many families of the Australian flora exist then as they do now? These questions are not easy to answer, and before investigating them it will be useful to give a rather detailed account of the Australian flora itself.

To begin with, it must be accepted that the evolution of the *families* of the flowering plants had begun in times earlier than those of the Upper Cretaceous period, for only a very few endemic families are found in Australia, and these have only a very few species in them. These families are the Akaniaceae, Balanopsidaceae (which also appears in New Guinea), Brunoniaceae, Byblidaceae, Cephalotaceae, and Tremandraceae. These are the only families that have developed endemically in Australia since the Upper Cretaceous period, although they might possibly have been preserved in Australia from times even more ancient than the Upper Cretaceous; since that period there has not been time enough for a further evolution of families. From this evidence we can conclude that it is very likely that the primitive ancestral types of the other, much larger, families of the Australian flora existed during the Upper Cretaceous period. If they had immigrated into Australia after Upper Cretaceous time—which is a possibility we naturally have to take into consideration—then they ought to be found in other parts of the world as well. We shall learn later in detail how far this is true. But, in any event, we must not assume that the six endemic Australian families also existed, at one time, in other parts of the world, only to die out later in those places, so that now they are native to Australia alone. We must be cautious with this kind of conclusion, a lesson which has been made obvious by the example of the mammals of New Zealand, referred to by Diels (1897) in his work on the vegetative biology of New Zealand. We shall return to this matter later in this paper.

According to A. Engler (1882), 425 of
the 1,393 genera of the Australian flora—
that is, 30.5 per cent—are endemic. This is
a statement of great importance, for from it
we learn that the time interval between the
Upper Cretaceous period and the present
time has been sufficient for the creation of
a great number of new genera—almost a
third of the genera found in Australia—or
for the conservation in Australia of a part of
them while in other continents they have be-
come extinct. It has already been stated that
the same suppositions are valid for 90 per
cent of all the Australian species. In short,
the period from Upper Cretaceous time until
the present has been long enough to create,
or, exclusively, to conserve, 30.5 per cent of
the *genera* and at least 90 per cent of the
species of the Australian flora. On the other
hand, it has not been long enough a time to
permit the creation, or the exclusive conser-
vation, of very many of the families of the
Australian flora, particularly of the larger
families.

It is interesting, for the sake of compari-
sons not unimportant to the arrival at a con-
clusion, to see how the species of the larger
groups are distributed in other parts of the
world. According to Hegi's *Flora* (1906–
1931), the larger groups of plants are repre-
sented in central Europe—Germany, Austria,
and Switzerland—by the numbers presented

TABLE 3

REPRESENTATION OF ENDEMIC SPECIES AMONG
THE LARGER PLANT GROUPS OF CENTRAL
EUROPE AND AUSTRALIA

PLANT GROUP	NUMBER OF SPECIES*	PERCENT-AGE OF "HIGHER FLORA"	COM-PARABLE FIGURES FOR AUSTRALIA
Pteridophytae	74	2.3	2.8
Gymnospermae	11	0.3	0.5
Monochlamydeae	355	11.2	12.8
Dialypetalae	1,043	32.9	41.2
Sympetalae	1,042	32.8	25.2
Monocotyledones	648	20.4	17.6

* According to Hegi (1906–1931).

in column 1 of Table 3. These figures are
converted, in column 2, into percentage val-
ues which can be compared with the figures
for the same plant groups in Australia
(column 3).

In several of these groups—the Pterido-
phytae, the Gymnospermae, and the Mono-
chlamydeae—the percentage values for Aus-
tralia do not differ much from those of central
Europe. In Australia the Monocotyledones
and the Sympetalae appear somewhat less
frequently than they do in Europe; while the
Dialypetales are found somewhat more fre-
quently in Australia than in central Europe.

In R. Mansfeld's catalogue of ferns and
flowering plants (1940), the figures given
for that part of central Europe included in
Germany, Austria, Bohemia, and Moravia are
presented in Table 4.

In northern Europe the Monocotyledones
are even more plentiful. In England they
form 25.3 per cent of the flora (Druce,
1932); in Iceland and the Faroes, 30.8 per
cent (Ostenfeld, 1934); in Greenland, 31.2
per cent (Ostenfeld, 1926); in Novaya
Zemlya, 33.3 per cent (Ekstam, 1897); and
in Spitzbergen, 31.2 per cent (Nathorst,
1883). In Portugal the Monocotyledones
form 20.3 per cent of the flora (Palhinha,
1939); in Italy, 18.6 per cent (Buscalione
and Muscatello, 1911–1913); in the Bal-
kans, 16.3 per cent (calculated from Hayek
and Markgraf, 1927–1933); and in the ter-
ritory of the Aegaean islands, 17.5 per cent
(calculated from Rechinger, 1943). It be-
comes apparent, then, that the number of
species of Monocotyledones is greater in
northern Europe than it is in southern
Europe.

With the Sympetalae quite the opposite
representation is found: the northern coun-
tries have fewer of these, the southern coun-
tries have more: Spitzbergen has 13.5 per
cent; Novaya Zemlya, 16.5 per cent; Green-
land, 21.1 per cent; the Faroes, 25.5 per
cent; England, 25.4 per cent; Germany, 29.5

PLANT GROUP	CENTRAL EUROPE*		AEGEAN ISLANDS†		PORTUGAL‡	
	NUMBER OF SPECIES	PERCENTAGE OF HIGHER FLORA	NUMBER OF SPECIES	PERCENTAGE OF HIGHER FLORA	NUMBER OF SPECIES	PERCENTAGE OF HIGHER FLORA
Pteridophytae	73	2.3	41	1.2	51	1.9
Gymnospermae	12	0.4	18	0.5	12	0.4
Monochlamydeae	332	10.4	368	11.2	305	11.0
Dialypetalae	1,119	35.2	1,154	35.0	994	36.0
Sympetalae	998	31.4	1,138	34.6	843	30.5
Monocotyledones	645	20.3	574	17.5	557	20.2
Totals	3,179		3,293		2,762	

*According to Mansfeld (1940). The unimportant differences between Hegi's figures and Mansfeld's may be ascribed to differences in criteria for the recognition of species as well as to the fact that Hegi's *Flora* included Switzerland and the South Tyrol while Mansfeld's did not.

†In his *Flora Aegaea,* Rechinger (1943) covers the territory of the Aegaean islands from Chalkidike in the north to Rhodes and Candia in the south.

‡The figures for Portugal are given by Ruy Telles Palhinha in his *Flora de Portugal* (1939).

per cent; Portugal, 30.5 per cent; Switzerland, 30.5 per cent; France, 31.2 per cent; Tyrol (including South Tyrol), 33.7 per cent; the Aegaean islands, 34.6 per cent; Italy, 35.7 per cent; the Balkan countries, 37.4 per cent. (These calculations are taken from A. Schmidt, 1944.)

When the figures for the endemics of Australia are compared with the figures for those parts of Europe which are rich in endemic plants, the contrasts are even more pronounced (Table 5).

From these comparisons we learn that endemic species of the Sympetalae are much more numerous in southern Europe than they are in Australia, and that, at the least, the centers of development of the polyphyletic Sympetalae are not likely to have been located in Australia. If they had been, the percentages of representation would have been reversed.

NUMBERS OF SPECIES IN FAMILIES

According to Mueller's figures (1889), which are approximately correct even today, the most important families in Australia, with respect to the numbers of their species, are these:

FAMILY	NUMBER OF SPECIES
Leguminosae	1,065
Myrtaceae	663
Proteaceae	597
Compositae	539
Cyperaceae	380
Gramineae	345
Epacridaceae	275
Orchidaceae	272
Euphorbiaceae	226
Goodeniaceae	220
Rutaceae	190

These eleven families, with a total of 4,372 species, include more than half of all the Australian phanerogams, of which there are 8,555 species. It is worth noting how remarkably the Leguminosae, Myrtaceae, Compositae, and Orchidaceae have developed. As we know, these families are by no means primitive. In this way the plants of the present Australian flora give evidence that their ancestors (related systematically) must have been well-developed at the time of the Upper Cretaceous period and even before.

The percentages of the endemic species in these 11 Australian families are tabulated as follows:

FAMILY	PERCENTAGE OF ENDEMIC SPECIES IN AUSTRALIA
Proteaceae	100
Epacridaceae	100
Goodeniaceae	99.9
Myrtaceae	98.3
(including all Leptospermoideae-Chamaelaucieae, all Leptospermoideae-Leptospermeae-Calothamninae, and all Leptospermoideae-Backhousiinae)	
Rutaceae	97.4
Orchidaceae	94.8
Compositae	91.5
Leguminosae	90.6
(including all Papilionaceae-Genisteae-Bossiaeinae)	
Euphorbiaceae	88.0
Cyperaceae	70.3
Gramineae	69.3

Of the larger families, 13 have only one species which has extended its range beyond Australia to other countries; these families are listed here, together with the number of species in each family which are found only in Australia:

FAMILY	NUMBER OF SPECIES IN AUSTRALIA
Myoporaceae	76
Haemodoraceae	66
Restionaceae	93
Dilleniaceae	95
Saxifragaceae	35
Magnoliaceae	18
Tremandraceae	17
Annonaceae	16
Stackhousiaceae	13
Coniferae	29
Cycadaceae	14
Casuarinaceae	24
Pittosporaceae	40

The Chenopodiaceae, with 111 species in Australia; the Hallorhagidaceae, with 58 species in Australia; and the Santalaceae, with 43 species in Australia, each has only two species which extend beyond the continent, and the Amaranthaceae, with 100 Australian species, has five species which extend their range beyond Australia to New Zealand and Polynesia. Of the smaller families, many have species appearing in territories other than the Australian, and are therefore without value in evaluating endemism in Australia:

FAMILY	NUMBER OF SPECIES IN AUSTRALIA	NUMBER OF SPECIES OUTSIDE AUSTRALIA
Nymphaeaceae	5	4 or 5
Guttiferae	4	3
Geraniaceae	8	5
Convolvulaceae	70	33
Lythraceae	19	12
Onagraceae	5	3
Rhizophoraceae	7	7
Cucurbitaceae	28	13
Hydrocharitaceae	9	7
Lemnaceae	6	6
Najadaceae Potamogetonaceae Aponogetonaceae	36	20

Many others of the smaller families might be added to this list, to support this contention.

THE PHYLOGENETIC AGE OF SYSTEMATIC GROUPS

Let us turn now to another question which is more easily answered: Do there exist, among the families of Australian plants, any

TABLE 5

COMPARISON OF PERCENTAGES OF ENDEMIC SPECIES IN THE HIGHER PLANT GROUPS OF AUSTRALIA WITH THOSE OF SOUTHERN EUROPE

PLANT GROUP	AUSTRALIA	ITALY	THE BALKANS	SARDINIA
Pteridophytae	1.6	0.5	0.0	4.2
Gymnospermae	0.5	0.0	0.2	0.0
Monochlamydeae	13.6	2.0	11.8	0.0
Dialypetalae	42.5	35.1	28.8	29.8
Sympetalae	25.8	56.4	49.9	55.3
Monocotyledones	16.0	5.9	9.3	10.6

of the larger systematic groups which are of very ancient age? The criteria for the recognition of phylogenetically old and new characteristics have been treated at length in my book (Suessenguth, 1938: 19 *et seq.*).

Let us consider the Leguminosae first. Among the members of the subfamily Mimosoideae the most important genus in Australia is *Acacia*, which has more than 300 Australian species. The rest of the genera of the Mimosoideae in Australia number only about 23 species.

Is the genus *Acacia*, then, an old or a new genus among the Mimosoideae? If we accept the general phylogenetic principle that free stamens are more primitive than fused stamens, and if we agree that the group of species with numerous stamens (now classified in the tribes Ingeae and Acacieae) is older than the group of species which have 10 or fewer than 10 stamens (now classified in the tribes Eumimoseae, Adenanthereae, Piptadenieae, and Parkieae), then we must conclude that the species of the tribe Acacieae, with their free stamens, are more primitive than are the more or less synantherous species of the tribes Ingeae and Parkieae. The Acacieae, with the genus *Acacia*—in which the filaments are free or only grown together to form a short ring—are undoubtedly the most primitive of the Mimosoideae, and apparently the plants of the genus *Acacia* are the most primitive of all of the Acacieae. Therefore, Australia shows the greatest number of oldest types among the Mimosoideae.

The subfamily Papilionatae presents much the same evidence. The most primitive tribes of the Papilionatae are those which have free stamens—the Sophoreae and the Podalyrieae. The Sophoreae generally have pinnate leaves, while the Podalyrieae have simple or digitate, rarely pinnate, leaves. Because of their simple leaves, the Podalyrieae may be considered the more primitive tribe. The Podalyrieae number 350 species in Australia, while

all of the other tribes of Papilionatae are far less numerous.

In summary, as far as the Leguminosae are concerned, it can be said that the Mimosoideae and the Papilionatae show the most pronounced development of primitive species in Australia.

Among the tribes of the Labiatae, the Prostanthereae are by far the most numerous in Australia, having 89 species compared with 31 for all of the other tribes. If we study the subfamilies of the Labiatae, as they are considered by Briquet (in Engler and Prantl, 1897), we come to the conclusion that the most primitive species must be those having no gynobasic pistil—the members of the tribes Ajugoideae and Prostantheroideae. When we investigate these two groups we learn that the Prostantheroideae have ovules with endosperm, while the Ajugoideae do not show any endosperm in their seeds—evidence that the Prostantheroideae are the most primitive of the Labiatae. These primitive Prostantheroideae are confined exclusively to Australia.

Among the Myrtaceae we think that the subfamily having dry fruits—the Leptospermoideae—is the most primitive. In Australia there are about 596 of these species with dry fruits, compared with only 41 species of Myrtoideae which bear berries. In Australia, then, the older subfamily has about 14.5 times as many species as does the younger one. The proportion of Leptospermoideae to Myrtoideae in the rest of the world is quite different: there are 678 species of Leptospermoideae and 1,932 species of Myrtoideae, a ratio of 1:2.85.

Among the Rutaceae the most primitive species are placed in the subfamilies which are inclined to apocarpy rather than in the subfamilies with united carpels (e.g., the Flindersioideae, Spathelioideae, Toddalioideae) or in those with bacciform fruits (e.g., the Aurantioideae). The Rutoideae show a tendency to apocarpy, and among their subfamilies several groups have developed: (a)

those with dorsiventral flowers (the American Cusparieae); (b) those without endosperms (the African Diosmeae); (c) those having herbaceous or suffruticose habit (the Ruteae of the northern temperate zone); and (d) those species with doubly digitate leaves (the Dictyolomeae of tropical South America). The remaining tribes of the Rutoideae are the Xanthoxyleae and the Boronieae. The Xanthoxyleae have a tendency to produce unisexual flowers, a characteristic which, for this group, is regarded as a derived feature. The most primitive types of the Rutaceae, then, are probably the Boronieae, and these types are limited to Australia and New Caledonia. In Australia there are about 143 species of the Boronieae and 26 species of the Xanthoxyleae, but only 9 species of the Flindersieae, 7 of the Aurantieae, and 3 of the Toddalieae. These figures, which could readily be supplemented with more evidence, show clearly enough that the primitive Rutaceae appear nowhere as plentifully as they do in Australia.

In considering the Loranthaceae, Engler (1894) mentions the Loranthoideae as the first state of development and the Viscoideae as the secondary one. The most primitive of the Loranthoideae are non-parasitic trees which have no berries—members of the genera *Nuytsia* and *Gaiadendron.* The species of *Nuytsia,* with dry false fruits, are considered more primitive than the species of *Gaiadendron,* with drupe-like false fruits. The species of *Nuytsia* are found only in western Australia. Of the four species of *Gaiadendron,* three are found in the Andes from Peru to Colombia, and one is found in eastern Australia.

Among the Dilleniaceae, two of the subfamilies, the Actinidioideae and the Saurauioideae, show a derived feature in the fusion of their carpels and further development in that the Actinidioideae and most of the Saurauioideae bear real berries. Neither of these subfamilies is represented in the Australian flora, the Actinidioideae being found in Japan, China, Manchuria, and the Himalayas, while the Saurauioideae are found in tropical Asia and America. All of the Australian species of the Dilleniaceae belong to the more primitive subfamily, the Dillenioideae. One of the tribes of the Dillenioideae, the Acrotremeae, is found outside of Australia, in India and Ceylon; but this is a less primitive tribe than is the Australian one, showing a number of derived characteristics, such as united carpels, a bushy habit, and pinnatipartite leaves. The other tribes of Dillenioideae—the Tetracereae, Hibbertieae, and Dillenieae—which also have representatives in southern Asia and tropical America, are not well enough known at present for a decision concerning the degree of their primitiveness or evolution.

Among the Restionaceae, the Diplanthereae have dithecic anthers and the Haplanthereae have monothecic anthers. Naturally, those genera with dithecic anthers are regarded as being the more primitive. They appear only in southwestern Australia; the genus *Anarthria,* with free anthers and a trilocular ovary, is the most primitive of them all. Among the Haplanthereae no differentiation can be made upon phylogenetic characteristics, for here the Australian and the African species share some characteristics. Nevertheless, the most primitive representatives do not appear outside of Australia.

The Centrolepidaceae show quite a similar relationship: among them, too, the species with dithecic anthers are also the more primitive ones. They are represented by the genus *Juncella* in southern Australia and in Tasmania.

The Goodeniaceae, although not completely endemic, have most of their representation in Australia. The most primitive genus in the family is *Calogyne,* which has bifid or trifid pistils. Two species of the genus are found in Australia and the third in south China.

Of the seven tribes of the family Proteaceae, the Persoonieae is the most primitive, as Engler has stated in his *Natürliche Pflanzenfamilien* (III/1: 127). The Persoonieae are found in Australia, Tasmania, New Caledonia, and, to a lesser extent, in New Zealand. One species of *Brabeium* appears at the Cape of Good Hope, but has developed farther than its relatives in Australia, as is proved by its floral axis which shows a cyathiform excrescence at the base. In any event, the most primitive representatives of the Proteaceae are almost completely limited to Australia.

In the Santalaceae, the members of the tribe Antholobeae, with their superior ovary, are considered primitive. The genus *Antholobus* is native to Australia. A closely related genus, *Exocarpus,* is found in Australia, Norfolk Island, the Malaysian islands, India, Madagascar, and Hawaii, although most of its species are native to Australia. The genus *Champereia* is found in Malacca and the Malaysian archipelago. It can be concluded, therefore, that the Santalaceae are of Australian-Malaysian—that is to say, of post-Gondwanesian—origin.

The most primitive Apocynaceae are those in which the stamens are not tightly connected with their stigma heads. These are the Plumieroideae, especially a subgroup of them, the Pleiocarpeae, which have apocarpic ovaries, pistils split at the base, and more than two carpels. Among them are two genera with the primitive arrangement of alternate leaves: *Notonerium* Benth., an ericoid bush growing in southern Australia, and *Lepinia* Decne., a tall tree found in Tahiti. The most primitive species of the Apocynaceae, therefore, are Australian-Pacific in their origin.

It might be noted in passing that this same conclusion cannot be drawn for the Asclepiadaceae. Here the Periploceae are the most primitive forms, judging by their tetrad pollen, the translators of which have no retinacula; and of these primitive Periploceae,

the most primitive are those which possess no corona, as, for example, the *Gymnolaima* of Kilimanjaro, Africa, the *Phyllanthera* of Java, and the *Pentamera* of Sumatra. The Asclepiadaceae are generally more highly evolved than are the Apocynaceae, but they do not originate in Australia.

Let us now go on to consider a rather complicated group, the Cyperaceae. Here the species of Scirpoideae, with their hermaphroditic flowers, are more primitive than are the Caricoideae, the flowers of which are rarely hermaphroditic. The nature of the axes in the inflorescences of the Caricoideae also proves to be a derived feature. Among the Scirpoideae there is a tribe, the Hypolytreae, whose members have bracted flowers; and the transverse arrangement of these bracts (as occurs among the Hypolytrinae) might be a more primitive characteristic than is the possession of one or two median bracts (as occurs among the Lipocarphinae). Among the Hypolytrinae the genus *Hypolytrum,* whose species show free bracts, is most primitive. A species of *Hypolytrum, H. latifolium* L. C. Rich., is found in Queensland, but it is also found in south Asia, Africa, America, and Polynesia. Two species of *Lipocarpha* also have an extensive range. The genus *Hypolytrum* has its representatives in the tropical and subtropical ranges of both hemispheres. All of this evidence would seem to show that the oldest living types of Cyperaceae—which is considered a rather "modern" family—have their native habitat in the tropics, but by no means in Australia.

In contrast to this, the oldest genus of the Scirpoideae-Cyperinae, the genus *Carpha* R. Br.—without disk, but with setaceous involucre, six setae, and a three-cleft pistil—is represented by one species from Australia and New Zealand and by another in extra-tropical Andean South America.

In the large subfamily of the Caricoideae, the Rhynchosporeae are the most primitive, inasmuch as, in most cases, they have three

anthers and an involucre. If we except the genus *Oreobolus*—which is somewhat in a special position because of its circum-Pacific distribution and its single, terminal, one-flowered false spikelets (Suessenguth, 1942) —we note that genera with alternate or very slightly distichous bracteal scales are more primitive than are those with distichous scales. Among these genera the most prim-itive are those which have three style branches and an involucre; of these genera three are especially worthy of consideration here:

> *Lepidosperma*, with nine-tenths of its species found in Australia, two in New Zealand, and two in tropical east Asia

> *Tricostularia*, with five-sevenths of its species found in Australia, one in Bor-neo, and one in Ceylon

> *Decalepis*, with one species found at the Cape of Good Hope in South Africa.

From this evidence we see that—again if we except the genus *Oreobolus*, which is of old-Pacific origin and which is difficult to classify —most of the oldest types of the Caricoideae are to be found in Australia, while the most primitive species of the whole family of the Cyperaceae are found in the tropics.

In order to complete the picture we should consider some of the families, the origin of which cannot be traced to Australia.

Of the Anacardiaceae the most primitive genus is *Buchanania*, native to tropical Asia, especially to the Malaysian territory, and to northern Australia. The most primitive spe-cies of *Buchanania* have four to six free car-pels, of which one is fertile.

The Compositae are impossible to trace to their origin, or to differentiate into their most primitive groups, even if we exclude from consideration the tribes which are ob-viously derived, like the Liguliflorae and the Mutisieae.

The family Cucurbitaceae is divided into the Fevilleae and the Fevillinae. The Fevil-leae are the more primitive, having five free anthers and loculamenta which are not grown together to form a circular ring (except for the slightly more developed Gomphogyninae and the Zanoninae, which have unilocular ovaries). The Fevillinae have trilocular ova-ries, and, of course, are more highly evolved than are the Fevilleae. All of these plants are native to tropical America, Brazil, and the West Indies.

Among the Orchidaceae, the more prim-itive species (the Diandrae-Apostasiinae) are not found in Australia. Species of the genus *Neuwiedia*, which have three fertile stamens, appear in Malacca and the Malaysian archi-pelago; those of the genus *Apostasia*, which have two fertile stamens, appear in the East Indies, the Malaysian archipelago, and trop-ical Australia. From this it is evident that the oldest types of the whole family belong to the tropics and are found today in terri-tories lying north of Australia.

The distribution of the Piperaceae (as, in-deed, of many another smaller family), leads us to expect a tropical origin for them.

Of the Rubiaceae, the more primitive sub-family is that of the Cinchonoideae, whose species have many seeds in each locule of the ovary. Among the Cinchonoideae, the Cinchoninae are more primitive because of their dry fruits. More highly developed groups, like the Condamineae and, to some extent, the Rondeletieae, have radiate flowers which are single or in panicles (but not in clusters), apterous seeds, whole or bipartite stipules, and the habit of trees or shrubs. The Rondeletieae, however, show imbricated or contorted vernation of the corolla, and the contorted vernation, at least, is a derived feature. Among the Condamineae the most primitive species are those in which the se-pals are of equal size and in which the petals are simply valvate and not reduplicatively valvate.

The simply valvate species are placed in the genera *Condaminea* (found in Andean South America), *Chimarrhis* (found in An-dean South America and in the Antilles),

Rustia (from Central America to Brazil), and *Tresanthera* (in Venezuela and in the West Indies). None of these genera even so much as appears in Australia. The reduplicatively valvate species of the Condamineae are placed in the genera *Portlandia* (found in the West Indies and in Mexico), *Isidorea* (in Haiti and Cuba), *Bikkia* (from the Pacific islands, New Caledonia, and Malacca), and *Morrierina* (found in New Caledonia).

Of the Rondeletieae, the simpler species, in which there is no contorted vernation of the corolla and in which the petals are not evolved into showy organs, are placed in the genera *Rhachicallis* (found in the Antilles), *Bathysa* (found in Brazil), and *Rondeletia* (found in the Antilles, Central America, and the northern parts of South America).

All of this evidence proves that the Rubiaceae did not originate in Australia, but primarily in the tropical regions of Central and South America and in the West Indies, and only in lesser part in the regions of New Caledonia and the Moluccas.

The most primitive species of the Valerianaceae appear on the Asiatic mainland: Species of *Nardostachys,* with four stamens and the clearly five-parted edge of the calyx, are found in the central Himalayas; species of *Patrinia,* with four stamens, extend westward from Japan through central Asia to the Ural mountains and northward into Arctic territory.

Now, in recapitulation, let us list all the larger systematic groups of the angiosperms, the most primitive types of which are found in Australia: Labiatae, Mimosoideae, Papilionatae, Myrtaceae (sub-family Leptospermoideae), Rutaceae, Santalaceae, Apocynaceae, Goodeniaceae, Proteaceae, Restionaceae, Centrolepidaceae, Loranthaceae, Dilleniaceae, Cyperaceae (subfamily Caricoideae). This summary and all of the evidence leading up to it are of great importance for the proper evaluation of many of the problems and questions in the science of plant geography.

Most of these groups cannot be considered primitive in the general phylogenetic sense—as, for example, these nine of the 14 families: the Labiatae, Papilionatae, Mimosoideae, Restionaceae, Centrolepidaceae, Apocynaceae, Myrtaceae, Goodeniaceae, and the subfamily Caricoideae of the family Cyperaceae. This would mean that the angiosperms which have developed in Australia since the Upper Cretaceous period cannot be traced back to the very earliest groups of angiosperms. These ancient groups must have developed in much earlier times than the Upper Cretaceous. It is not likely that the nine families have spread from Australia to other parts of the world *after* Australia's geographic isolation began and that the original primitive species have been conserved in Australia ever since that time. On the contrary, it is much more probable that the primitive ancestral types also existed in other parts of the world even before the Upper Cretaceous period and that they have died out there since that time, just as most of the Marsupialia and the Monotremata have died out in parts of the world outside of Australia. Finally, it should be remembered that it is also possible that the Australian angiosperms of today might have had ancestors originating in other continents before the beginning of Australia's geographic isolation.

It is likely, too, that many of the families of the Australian plants have migrated into Australia in times later than the Upper Cretaceous period, especially those families found now in northern, tropical Queensland.

All of this would mean that parent types of most of the derived families of Angiospermae were already in existence before the Upper Cretaceous period, and that the development of the main branches of the Angiospermae took place in even earlier times. Fossil discoveries lead us to suppose that a strong and rapid development of angiosperms has taken place since the Upper Cretaceous period. Investigations of the

Australian flora do not confirm this impression, however. Rather, they support the supposition that, in most of its essentials, the development of flowering plants goes back to even earlier times—to the period of Lower Cretaceous formations, possibly even as far back as the Jurassic period. Unfortunately there are not many fossil evidences of angiosperms preserved from Jurassic times, and very few of these can be identified with certainty. When the Cenozoic era began, the chief development of the angiosperms must already have been finished. Particularly primitive types might have been preserved until then, of course, but there is no definite fossil evidence as yet of this possibility.[2]

COMPARISON OF AUSTRALIA WITH NEW ZEALAND

In this connection it might be significant to draw a parallel by investigating a land area near Australia and which has been isolated from other continents for even a longer time than Australia. Such a territory is New Zealand. No fossil mammals were found there, while, as we know, primitive mammals had entered Australia from southern Asia. In the event that some of these mammals originated in Australia itself—a rather untenable supposition—they must have wandered out of Australia over land bridges toward the north, eventually to reach Europe and North America. In New Zealand, on the other hand, only a small rat has been found to represent the mammals, and this rat was probably imported by man

in very recent times. The islands of New Zealand have never been connected with land areas inhabited by mammals, and until now no fossil relics of mammals have been found there; it is very unlikely, therefore, that mammals did live in New Zealand at one time but have died out there since.

Now, if New Zealand has never been connected with land areas populated by mammals, where did its flora come from? And does this flora show still more primitive features than does that of Australia?

Diels (1897) has entered into a full discussion of these questions in his work on the *Vegetationsbiologie von Neuseeland.* He assumes that New Zealand has not been submerged since the middle of the Mesozoic era. According to Hutton (cited by Diels, 1897), New Zealand was connected with an Antarctic continent which existed during the Lower Cretaceous period, toward the end of the Mesozoic era. Diels thinks it is probable that, even during the later Triassic period in early Mesozoic time, the Austral circumpolar lands were closely related to each other, so that there was a genetical connection among the mountain floras of Tasmania, southern Australia, the southernmost part of South America, and an Antarctic continent which probably was more temperate in its climate in those early times than it is now. This interrelationship of floras would find its parallel in the Arctic, Alpine, and Altaic floras of the northern hemisphere.

In his paper, Diels cites evidence to support this supposition of the connection of the Antarctic and Austral land masses. In those times the Antarctic continent must have been much larger than it is today, free from ice in its northern parts, and certainly warmer during the Triassic period. In addition to Diel's evidence, we can find further testimony in comparative zoology and in plant geography. Fossil relics of marsupial groups now limited to Australia—species of the

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[2] Erdtman in 1948 published reports in *Grana Palynologica,* that pollen had been found in the black lias formations of southern Sweden. The pollen appears similar to that of *Eucommia* species (*Eucommia* is a genus in China, closely related to the Ulmaceae) and it is not likely to have been derived from Gymnospermae. Inasmuch as the black lias of Sweden is a Lower Jurassic formation, these pollen finds may offer some evidence of the early development of the angiosperms.

Abderitidae, and of the Sparassodontidae, which are related to the Dasyuridae—have been discovered in Eocene deposits in Patagonia; and Zittel (1895) concluded that "it is an undeniable paleontologic fact that in those times both regions were in mutual exchange or at least drew from the same sources." But only the western isle of the former Australian archipelago (the West Australia of today) participated in this exchange. The eastern islands, particularly New Zealand, did not—because they were not connected either with western Australia or with Patagonia. The most primitive species of marsupials—species of *Myrmecobius* and *Peragalea*—are endemic to West Australia, and it is a very significant fact that there is no fossil evidence to prove that marsupials existed in eastern Australia at any time before the late Cenozoic era, that is to say, before the central Australian sea had retreated (Zittel, 1895: 294). All this is evidence that there must have been connecting land links between Patagonia and western Australia.

We find a very interesting parallel in the distribution of two sections of the genus *Discaria* of the family Rhamnaceae. The section *Notophaena* (Miers) Suessenguth, in its present range, connects Chile and New Zealand. The section *Eudiscaria* Stapf appears in the Argentine countries (that is, in the countries east of Chile), and in Tasmania, Victoria, and New South Wales. This distribution can be explained only by assuming two land bridges leading through an Antarctic continent—one connecting Chile and New Zealand, in a strip slightly arched towards the south; another, farther south than the first, leading from eastern Patagonia through the Antarctic continent to Tasmania and southeast Australia.

It is my opinion that all sketches of these hypothetical land bridges which have been published are not quite correct, for it is impossible—for phytogenetical as well as pale-

ographical reasons—that the connection from Chile to east Australia could have been formed in a straight line. On the contrary, this line passed farther south through an Antarctic continent, which at that time was overgrown with plants.

According to Hutton and Wallace (cited by Diels, 1897), a Melanesian continent connecting New Caledonia, Lord Howe Island, Norfolk Island, and New Zealand, and reaching as far north as the present north Queensland, might well have existed in the Eocene epoch. There was no connection, however, between this continent and western Australia. In Miocene times west Australia and east Australia were connected, but the west Australian species never reached the tropics, and, therefore, did not get to New Zealand.

From these few considerations we learn that the situation in New Zealand is quite different from that in Australia. New Zealand was closely related to the Antarctic continent and to a Melanesian continent, but we cannot expect to find there the primitive species of the Australian continent. The different character of the flora of New Zealand is proof of this expectation. In their *Manual of the New Zealand Flora,* Cheeseman and Oliver (1925) list 1,591 species of vascular plants, with 1,415 phanerogams and 156 vascular cryptogams, among all of which are 1,143 endemic species—72.8 per cent—and 24 endemic genera. While Mueller's catalogue counts 592 species of Proteaceae in Australia, only two can be listed for New Zealand. The large Australian genera of *Eucalyptus* and *Acacia* are completely missing in New Zealand. The floristic connection of New Zealand with Australia is formed by certain of the Myrtaceae (the genus *Metrosideros*) and by the family Epacridaceae. According to Grisebach (1872: II, 633) these are the New Zealand families or groups which are represented by the most species:

PLANT GROUP	NUMBER OF SPECIES	PERCENTAGE OF VASCULAR PLANTS REPRESENTED BY GROUP
Compositae	221	14.1
Ferns	138	8.8
Cyperaceae	119	7.6
Scrophulariaceae . . .	113	7.2
Gramineae	113	7.2
Umbelliferae	62	3.9
Orchidaceae	57	3.6
Ranunculaceae	50	3.2
Rubiaceae	47	3.0
Epacridaceae	31	2.0
Onagraceae	31	2.0
Leguminosae	26	1.7
Juncaceae	25	1.6
Boraginaceae	25	1.6

The differences between the figures for New Zealand and those for Australia are very striking: Leguminosae, ranking first in Australia, is not among even the first 10 of the families of New Zealand, and neither is Myrtaceae (in second place in Australia), Proteaceae (in third place), or Euphorbiaceae (in eighth place). The Compositae, however, have achieved first place in the New Zealand flora (they are in fourth place in Australia), and—the ferns being left out of consideration—the Scrophulariaceae, the Umbelliferae, the Rubiaceae, and the Ranunculaceae have entered into the list of families with the most species. The Labiatae, in contrast, are not to be found at all in New Zealand; they did not reach these islands from Malaysia and Australia.

Of the 1,591 plant species found in New Zealand, 428 species are not endemic. Among these, 366 are related to the Australian flora, and 108 are related to that of South America.

The genera with the greatest number of species in New Zealand are these: *Veronica,* 84 species; *Carex,* 54; *Celmisia,* 43; *Coprosma,* 40; *Ranunculus,* 38; *Olearia,* 35; *Senecio,* 30; *Epilobium,* 28; *Poa,* 25; *Myosotis,* 23; and *Hymenophyllum,* 20.

It cannot be said, however, that New Zealand's flora is more primitive or has more primitive species than does the flora of Australia, even though its isolation from Malay-

sia and New Guinea apparently occurred earlier than did that of Australia. The great number of endemics in New Zealand's flora, then, can be attributed not to the conservation of primitive species, but rather to the formation of new ones.

Because of its temporary connection with Australia, Melanesia, and the Antarctic continent, New Zealand cannot give us any assistance in solving the problem of the origin of the larger and older Australian flora, so important in any estimation of the age of the angiosperms. The geologic and biologic records left on New Zealand are quite different from those of Australia, and they can not be traced very far back into geologic time.

ORIGIN OF NEW TYPES IN AUSTRALIA

How, then, can we explain the appearance of new types in Australia? Perhaps the following supposition may be the simplest one.

Let us assume that during the Upper Cretaceous period, or possibly during the Middle Cretaceous period, but in any case a short time before Australia's geographic isolation began, there existed the plant types A, B, C, D . . . *in Malaysia as well as in Australia.* Since that time, the Malaysian types have evolved into types A^1, B^1, C^1, D^1 . . . that is, into new and different species or genera. The Australian types, however, have developed into types A^2, B^2, C^2, D^2 . . . into different species or genera from both their parent types, A, B, C, D . . . and the collateral types A^1, B^1, C^1, D^1 . . . developing in Malaysia. It is conceivable that the endemic plants in Australia have evolved in this manner.

Of course it is also possible that this development of endemics could have taken place in later times, without it being necessary for us to conclude that all species of the parent series A, B, C, D . . . must have been distributed throughout Malaysia and

Australia during the Upper Cretaceous period. Many of them may have migrated to Australia in later times, after the separation, and may have evolved there into types A^2, B^2, C^2, D^2. . . . But if this is true of some plants, it is not likely to be true of the Leguminosae: It is probable that the primitive species of the Mimosoideae, the Papilionateae, and of some of the *other* families listed above (p. 295) immigrated into Australia a long time ago and have survived there unchanged, remaining generally identical with their ancestors of the Upper Cretaceous period, wherever these ancestors may have grown.

For some of the other plant groups, it is possible that their species A^2, B^2, C^2, D^2. . . may have risen in different epochs. A^1, B^1, C^1, D^1. . . in Malaysia, and A^2, B^2, C^2, D^2. . . in Australia, continued to live, while their common ancestors A, B, C, D. . . died out in both territories. Or, if we assume that $A^1 = A$, $B^1 = B$, $C^1 = C$, and so on, or if we take $A^2 = A$, $B^2 = B$, $C^2 = C$, and so on, we might deal, then, with only two lines of development instead of three, and only one of them need have changed—either the one in Australia, since the beginning of its isolation, or the line in Malaysia, since Australia's separation. In other words, the local ancestors of the line A, B, C, D. . . might have died out in one territory and might have been preserved in the other for a very long time. Yet this is not very probable a chance inasmuch as most species of living things—except for the mussels—generally have not been conserved unchanged over long periods of geologic time.

In my opinion this line of approach is the most natural way of explaining the problem. It does not relegate the appearance of all the endemic families of the Australian angiosperms to the apocryphal darkness of antiquity, and yet it does help us to understand the rise of the many endemics in Australia. If we do not insist that all of

these developments took place at almost the same time (in the Upper Cretaceous period) and if we agree that the possibility of subsequent immigrations into Australia must also be taken into account, then we would do well to remember that in their manner of distribution angiosperms and mammals differ markedly in at least this major point: Flowering plants are much more able to cross the sea—if only by means of driftwood—than are mammals. This would seem to be an assertion that could hardly be contested. And yet it is a strange fact that greater numbers of primitive plant types have not been preserved. They became extinct, while the primitive types of animals—the Marsupialia and Monotremata—continued to live. These animals link the mammals with the reptiles, but even at the present time no plants are known in Australia which link the angiosperms with the gymnosperms. The botanical systematist will regret this fact, if only because such proof of primitiveness would be a much more scientific, and therefore a more reliable, basis for the taxonomic system.

My impression of the rise of Australian endemics has been described with reference to its relationship to Malaysia, both because the endemics of this area are more closely related to those of Australia and because of Australia's former connection with New Guinea (see Behrmann, 1937). Perhaps these conclusions will seem quite natural to most readers; nevertheless, I think it would be useful to develop further conclusions based on certain concrete suppositions.

As has been known for a long time, most of the species of the plant families characteristic of Australia grow in the southwestern maritime areas (Hooker, 1860). Fewer species are found toward the north. According to his catalogue, Hooker counted 3,600 species in the southwestern territory, known in his day as Swan River and King George Sound, but only 3,000 from the eastern area,

and only 2,200 from tropical Australia, where the endemic species are fewest in number. Now what is the reason for this distribution? Is it because Malaysia has exerted less of an influence upon these southwestern districts because they are so distant, and because they are separated from the interior—and therefore from the northern shores and Malaysia—by vast deserts? Is this pronounced isolation the reason why more endemic species have developed and have been preserved in the southern periphery of Australia than in its other parts? Or is there a more general rule, as yet unexplained, that endemics are developed more generously in southern lands?

If we compare South Africa with Australia, we can count an enormous number of endemics in Cape Colony; and if we compare the most southern parts of South America—Patagonia and Chile—with Australia, we can find there, too, a great number of endemic species—1,200 of 1,600 species, according to Grisebach's early evaluation in his *Die Vegetation der Erde* (1872: II, 498).

It is not possible to indicate a preponderance of endemisms in the most southern part of India, at least on the basis of the figures reported by Hooker and Thomson in their *Introduction to the Flora Indica* (1855). Newer statistics concerning Indian endemisms apparently are not yet published.

In Europe, however, the majority of endemics is found in the southern areas, particularly in the Balkans and in Crete (Turrill, 1929). In this connection, Newbigin (1936) has made these statements about mammals: "It has been made abundantly clear that the great migratory movements have been from the wide land masses of the northern hemisphere towards the narrower and discontinuous southern ones, and that extinction of early stocks has been most marked in the Holarctic region, while the survival of members of these is especially characteristic of some of the southern lands. . . . The past and present distribution of the higher plants con-

firms the conclusions derived from the study of mammals. Sometimes the correspondence is curiously exact." Unfortunately, Newbigin does not give his proofs of these lapidary sentences, particularly for the plants. Let us, therefore, find our own proofs in some examples from the pertinent literature.

A good many of the flowering plants, as, for example, the families of the Papaveraceae and the Geraniaceae, have migrated along the ridges of the Andes, from both North America and Central America, far into South America (Vester, 1940: 162, fig. 78). The genus *Ribes,* which also migrated in this manner, has been cited for this fact by Newbigin (1936). The same evidence of migration appears to be provided for some of the Primulaceae, with *Primula farinosa* in the Holarctic region and in Andean Patagonia (Vester, 1940: 154, fig. 40); for the Betulaceaè (*ibid.,* 163, fig. 80); for the Empetraceae (*ibid.,* 163, fig. 81); for the Orobanchaceae (*ibid.,* 164, fig. 86); and for the Juglandaceae (*ibid.,* 176, fig. 153).

Fossil discoveries give further evidence that, to a great extent, some of the plant groups were forced out of northern areas into southern not only by diluvial glaciers, which, coming from the north, destroyed the Cenozoic flora of central Europe and of central North America, but also by hitherto unknown factors which were effective much farther southward. The Magnoliaceae, for instance, at one time must have grown over vast parts of the Holarctic region, but today they are limited to South and Central America, eastern and southeastern North America, the West Indies, southwestern Asia, Malaysia, eastern Australia, and New Zealand (Vester, 1940: 188, fig. 262). The Juglandaceae, too, have disappeared from large areas of northwestern North America, from Europe (except for the Balkans), and from central Asia (except for the Caucasus), while in the more southern regions they continue to survive. Further examples are to be found in the fam-

ily Ebenaceae, according to Fernald (*in* Vester, 1940: 174), and in the tribe Cycadeae and the genera *Podocarpus* and *Araucaria,* according to Studt (1926).

It is doubtful whether any instances can be found to prove a considerable migration of a plant flora in the opposite direction, that is, from south to north. It is true, of course, that a number of plants, reported by Suessenguth (1942), have worked their way northward from the South American Andes, reaching as far north as Costa Rica and Mexico. However, these migrations have taken place only since the Miocene elevation of the Cordilleras in Central America, and they are rather insignificant compared with the major southward migrations.

There is evidence, however, that northeastern Africa has been reached from a northeastern direction by species of plants from India and western Asia.

Although it might be expected that the Mediterranean floral elements might have arrived in central Europe from the south, following the retreating glaciers as they withdrew to the north, I do not think this argument is tenable, inasmuch as it is quite possible that representatives of the Mediterranean flora might have found refuges in the climatically favorable parts of central Europe during the glacial advances. It is much more likely that the North American plants of Cenozoic time were forced southward by the glaciers, and then, after the glaciers had retreated, were permitted to return north, to recover vast territories of their former areas of distribution. Nonetheless, these instances of northward migration are abundantly surpassed by the notable removal to the south of plants in Australia, the Andes, Patagonia, Cape Colony, and the Balkans, in all of which real displacements to the south have been demonstrated. During the cold periods of the glacial advances, all of the hydro-megatherms and megatherms should have been concentrated towards the tropics from the Arctic and Antarctic regions, and it is not to be denied that a large part of the "small belt-like areas" of many families in the whole tropic range may thus have been established in their present ranges (Vester, 1940: 166 *et seq.,* figs. 93–113). Nevertheless, it seems as if in Australia, the Andes, Africa, and Europe other factors had contributed to force a great number of species of plants from the north to the south, and in those areas in the southern hemisphere this displacement carried the plants even farther south than the Tropic of Capricorn.

This phenomenon of displacement from north to south does not need the supposition of some mystical power to explain it. In Africa, for example, a northward counter-displacement of the ancient flora of the northern and middle part of the continent could not happen because it was blocked in that direction by the broad Tethys sea of the early Tertiary period (Eocene time, and so on) or by the deserts that are its relics. Australia, to give another example, in post-Tertiary time could not receive plants from any direction but from the north, because it was only there that Australia was connected, if only temporarily, by land bridges with large masses of land, while in the south the Antarctic continent at a later period was too cold and too far distant to permit of plant migration. In the Andes plant distribution is not as easily explained. In the Balkans the lowering of temperatures in the north by the glaciers may have played a part in the southward displacement of the plant life, so that numerous types of plants died out in the north which continued to live in the south. It would be of great interest to investigate the degree of displacement in still other parts of the world.

Many other objections might be raised to dispute this claim of the southward displacement of plants. The major point of dispute is whether or not this southward displacement of certain systematic groups—such as,

for example, the Magnoliaceae, which are said to be analagous in this respect to many animal groups—can be attributed only to the lowering of temperatures in the northern regions during the time of glaciation.

CONCLUSION

These investigations have offered statistical evidence that the phylogenetically older types of about 10 large taxonomic groups of the higher plants are found, either exclusively or in their great majority, in Australia. By analyzing the floras of the lands near Australia today, and by drawing analogies from the floras of the southern parts of all of the other continents, it can be concluded that the ancestors of the Australian plants must have existed in Australia during the times of the Upper Cretaceous period. This can be the only conclusion because it would be impossible for the Australian flora to form one vast atavism, if only because atavisms are rare, when they are encountered at all, and usually play no part in the formation of species.

It should be stressed that in order to reach this conclusion no contrived assumptions were made regarding the primitiveness of the characteristics of the Australian plants: Concepts and judgments of primitiveness were based entirely upon the well-established criteria of the older taxonomic systems (the *Natürliche Pflanzenfamilien* of Engler and Prantl, for example) and upon the general discussions of phylogenetically important characteristics given by Wettstein in his handbook of systematic botany (1935) and by myself (Suessenguth, 1938), without dependence upon rules or criteria established particularly for the Australian flora. The special questions of the phylogenetic age of Australian families put in this paper, and the answers proposed to them, have not been presented before, to my knowledge.

The data obtained in these investigations would suggest that natural immigrations of plants into Australia, after the beginning of its isolation from Malaysia, were not very likely—or at least were not very plentiful—the enormous degree of endemism which Australia now exhibits being evidence against any considerable change in later times.

It cannot be established with certainty whether or not the plants of the primitive genera of the 10 major Australian families are not only endemic by preservation but are also plants which have originated in Australia and which have existed there since their beginning to become the ancestors from which the families have spread throughout the world. In the majority of cases I do not think it likely that these plants have been disseminated from an Australian center inasmuch as paleontological evidence concerning animals shows that many animals which at one time were widely distributed have been preserved alive in Australia while they have become extinct in other regions. Obviously, what has happened to animals could also have happened to plants.

We can conclude, however, from the indirect evidence presented by the Australian flora that the development of primitive families of the angiosperms must have taken place during the Middle and Lower Cretaceous period or, possibly even earlier, during the Jurassic period. But this conclusion, while it is supported by the endemic nature of the Australian flora—which, of course, was isolated when the connection of Australia with Malaysia was ended in the Upper Cretaceous period—has yet to be confirmed by the discovery of fossil evidences of angiosperms in formations of those Middle Mesozoic times.

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